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WOOD ANATOMY OF CHLOANTHACEAE (DICRASTYLIDACEAE)

Sherwin Carlquist¹

Introduction

Chloanthaceae, apparently the correct name for a group also termed Dicrastylidaceae (Munir 1978), is a familial taxon often used for Australian genera which have been referred to Verbenaceae. The family was erected by Hutchinson (1959). Others have, to be sure, treated the family as a distinct tribe of Verbenaceae, beginning with Bentham and Hooker (1876). The presence of endosperm in seeds as well as ovule position in Chloanthaceae have been used as criteria for segregating the family from Verbenaceae (Munir 1979). However, the present study adds two important distinctions. All species of Chloanthaceae examined to date have successive cambia. Verbenaceae have normal cambia except for *Avicennia* (Metcalfe and Chalk 1950; Zamski 1979), a genus sometimes recognized as a separate family. Chloanthaceae all prove to have bordered pits on imperforate tracheary elements of the secondary xylem. These pits are not fully bordered; they are intermediate between fully bordered and vestigially bordered. Thus the elements should be termed fibertracheids. Vestigial borders have been reported on pits of imperforate tracheary elements of *Petraea volubilis* L. (Metcalfe and Chalk 1950) and *Tectona* (Gottwald and Parameswaran 1980), but all other nonchloanthoid Verbenaceae have simple pits on imperforate tracheary elements according to Metcalfe and Chalk.

Thus, Chloanthaceae have more distinctive characters than previously recognized, and the segregate family is used in the present paper as a way of calling attention to these characters. The taxonomic groupings of genera into families within the tubiflorous families of dicotyledons may be expected to shift. Among authors who have recognized Chloanthaceae (some under the name Dicrastylidaceae) as a family are Airy Shaw (1965), Beard (1970), Eichler (1965), Gardner (1972), Maconochie and Byrnes (1971), Moldenke (1971), Munir (1975, 1978, 1979), Symon (1969), and the editors of *Index Kewensis*. A case could easily be made that Chloanthaceae are as distinct from Verbenaceae as are Lamiaceae. The presence of borders on pits of fiber-tracheids and the presence of endosperm may be considered primitive features in tubiflorous dicotyledons. The occurrence of successive cambia is very likely a specialized feature, one which perhaps suits attainment of greater stature in taxa where moderate conditions permit larger-sized plants. One might hypothesize that the ancestor of chloanthoids was a short-lived plant with little cambial activity, like the *Dicrastylis* species of desert areas

of Australia, and that the woody habit was acquired, accompanied by innovation of successive cambia, as that chloanthoid stock moved into more moderate habitats.

In the present study, wood anatomy of Chloanthaceae is considered, but the nature of the successive cambia which produce the wood is not studied. That topic needs investigation. The number of species in the present study is not notably large. Stems of most species develop little wood, and such a genus as *Mallophora*, although a subshrub, produces only slender twigs unsuitable for study. Wood samples of chloanthoid genera are not to be found in wood collections, the focus of which is almost invariably arboreal species of dicotyledons. The stems I collected were at least 5 mm in diameter. Most of these show an irregular surface rather than a smooth cylindrical conformation. As in certain other dicotyledonous groups, the irregular surface is an indication of the occurrence of successive cambia. The products of these cambia occur as arcs which often do not extend around the entire circumference of a stem.

The species studied here were collected in Northern Territory in 1978 (*Pityrodia jamesii* Specht, *P. lanceolata* Munir, *P. lanuginosa* Munir) or in southwestern Australia in 1974 (remaining species). The three Northern Territory wood collections were made during a helicopter reconnaissance of the Arnhem Land sandstone plateau. *Pityrodia jamesii* and *P. lanuginosa* were collected at "Camp 2" whereas *P. lanceolata* was collected at "Camp 3"; details of this expedition are given in an earlier paper (Carlquist 1979). *Cyanostegia angustifolia* Turcz. was collected in a sand area near Kalbarrie. The other collections were made in areas closer to the coast. Chloanthaceae are a characteristic element of the sandplains of southwestern Australia. The occurrence of the Northern Territory *Pityrodia* species on sandstone represents an ecologically similar situation with respect to substrate. The lack of wood development in chloanthoids of southwestern Australia may be attributed to summer heat and drought, or possibly winter frost in some species. Either of these factors would tend to result in the innovation of branches from the ground level each year. In the Northern Territory *Pityrodia* species, however, the growing season is yearlong, so that woody trunks, as in *P. lanceolata*, and stature as small trees can be achieved. *Pityrodia jamesii* and *P. lanuginosa* are shrubs more than a meter in height but of limited duration. This trio of species shows some correlation between plant size and mesomorphy; *P. lanceolata* is the largest plant of the three, and it also has the largest leaves (Fig. 28). Anatomical literature contains virtually no information on wood anatomy of Chloanthaceae.

Materials and Methods

Wood samples were collected in the field and dried. Liquid preservation is a more advisable procedure with woods involving successive cambia;

however, details of secondary phloem and parenchyma between vascular bands in stems were often not at all seriously damaged as a result of drying (e.g., Fig. 1, 3, 4, 12). Wood samples were boiled and sectioned on a sliding microtome. Macerations were also prepared from the boiled wood segments. Safranin was used as a stain for both the sections and the macerations.

Quantitative Data

Quantitative data were prepared according to the usual methods. However, the figure for vessels per sq. mm. refers to xylem areas per se, and does not result from a scan including parenchyma bands between the vascular tissue. The calculations for V ("vulnerability") and M ("mesomorphy") are based upon formulas presented earlier (Carlquist, 1977).

Cyanostegia angustifolia Turcz (*Carlquist s.n.*). Mean vessel diameter, 36 μm . Vessels per sq. mm., 252. Vessels per group, mean, 5.36. Mean vessel-element length, 257 μm . Mean fiber-tracheid length, 456 μm . Fiber-tracheid wall thickness, 2.6 μm . Mean multiseriate ray height, 282 μm . Mean uniseriate ray height 141 μm . $V = 0.14$; $M = 36$.

Cyanostegia lanceolata Turcz (*Carlquist* 5905, RSA). Mean vessel diameter, 36 μm . Vessels per sq. mm., 221. Vessels per group, mean, 3.24. Mean vessel-element length, 274 μm . Mean fiber-tracheid length, 526 μm . Fiber-tracheid wall thickness, 2.8 μm . Mean multiseriate ray height, 392 μm . Mean uniseriate ray height, 293 μm . $V = 0.14$; $M = 44$.

Lachnostachys eriobotrya (F. Muell.) Druce (*Carlquist* 5896, RSA). Mean vessel diameter, 34 μm . Vessels per sq. mm., 155. Vessels per group, mean, 2.60. Mean vessel-element length, 266 μm . Mean fiber-tracheid length, 556 μm . Fiber-tracheid wall thickness, 2.5 μm . Mean multiseriate ray height, 639 μm . Mean uniseriate ray height, 439 μm . $V = 0.22$; $M = 59$.

Physopsis lachnostachys C. A. Gardner (*Carlquist* 5975, RSA). Mean vessel diameter, 36 μm . Vessels per sq. mm., 109. Vessels per group, mean, 1.88. Mean vessel-element length, 201 μm . Mean fiber-tracheid length, 420 μm . Fiber-tracheid wall thickness, 3.0 μm . Mean multiseriate ray height, 701 μm . Mean uniseriate ray height, 270 μm . $V = 0.33$; $M = 66$.

Pityrodia bartlingii (Lehm.) Benth. (*Carlquist* 5483, RSA). Mean vessel diameter, 44 μm . Vessels per sq. mm., 171. Vessels per group, mean, 6.28. Mean vessel-element length, 252 μm . Mean fiber-tracheid length, 473 μm . Fiber-tracheid wall thickness, 3.0 μm . Mean multiseriate ray height, 667 μm . Mean uniseriate ray height, 307 μm . $V = 0.26$; $M = 65$.

Pityrodia jamesii Specht (*Carlquist* 15417, RSA). Mean vessel diameter, 40 μm . Vessels per sq. mm., 98. Vessels per group, mean, 1.50. Mean vessel-element length, 269 μm . Mean fiber-tracheid length, 516 μm . Fiber-tracheid wall thickness, 2.6 μm . Mean multiseriate ray height, 371 μm . Mean uniseriate ray height, 160 μm . $M = 0.41$; $V = 110$.

Pityrodia lanceolata Munir (*Carlquist 15450*, RSA). Mean vessel diameter, 38 μm . Vessels per sq. mm., 126. Vessels per group, mean, 3.36. Mean vessel-element length, 296 μm . Mean fiber-tracheid length, 472 μm . Fiber-tracheid wall thickness, 3.1 μm . Mean multiseriate ray height, 417 μm . Mean uniseriate ray height, 162 μm . $V = 0.30$; $M = 89$.

Pityrodia lanuginosa Munir (*Dunlop 4913*, RSA). Mean vessel diameter, 44 μm . Vessels per sq. mm., 134. Vessels per group, mean, 2.24. Mean vessel-element length, 358 μm . Mean fiber-tracheid length, 600 μm . Fiber-tracheid wall thickness, 2.7 μm . Mean multiseriate ray height, 700 μm . Mean uniseriate ray height, 355 μm . $V = 0.33$; $M = 118$.

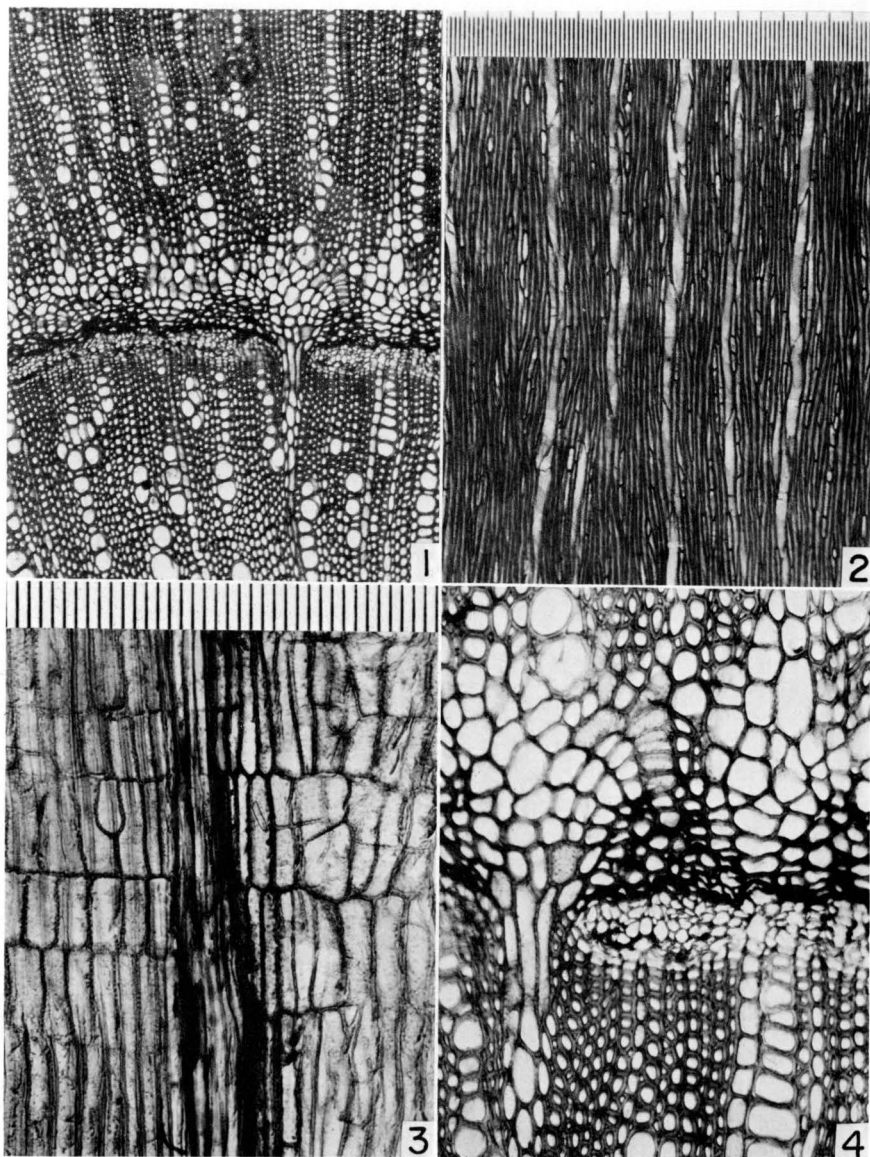
Pityrodia oldfieldii (F. Muell.) Benth. (*Carlquist 5899*, RSA). Mean vessel diameter, 36 μm . Vessels per sq. mm., 93. Vessels per group, mean, 2.92. Mean vessel-element length, 210 μm . Mean fiber-tracheid length, 496 μm . Fiber-tracheid wall thickness, 3.5 μm . Mean multiseriate ray height, 635 μm . Mean uniseriate ray height, 243 μm . $V = 0.39$; $M = 80$.

Anatomical Descriptions

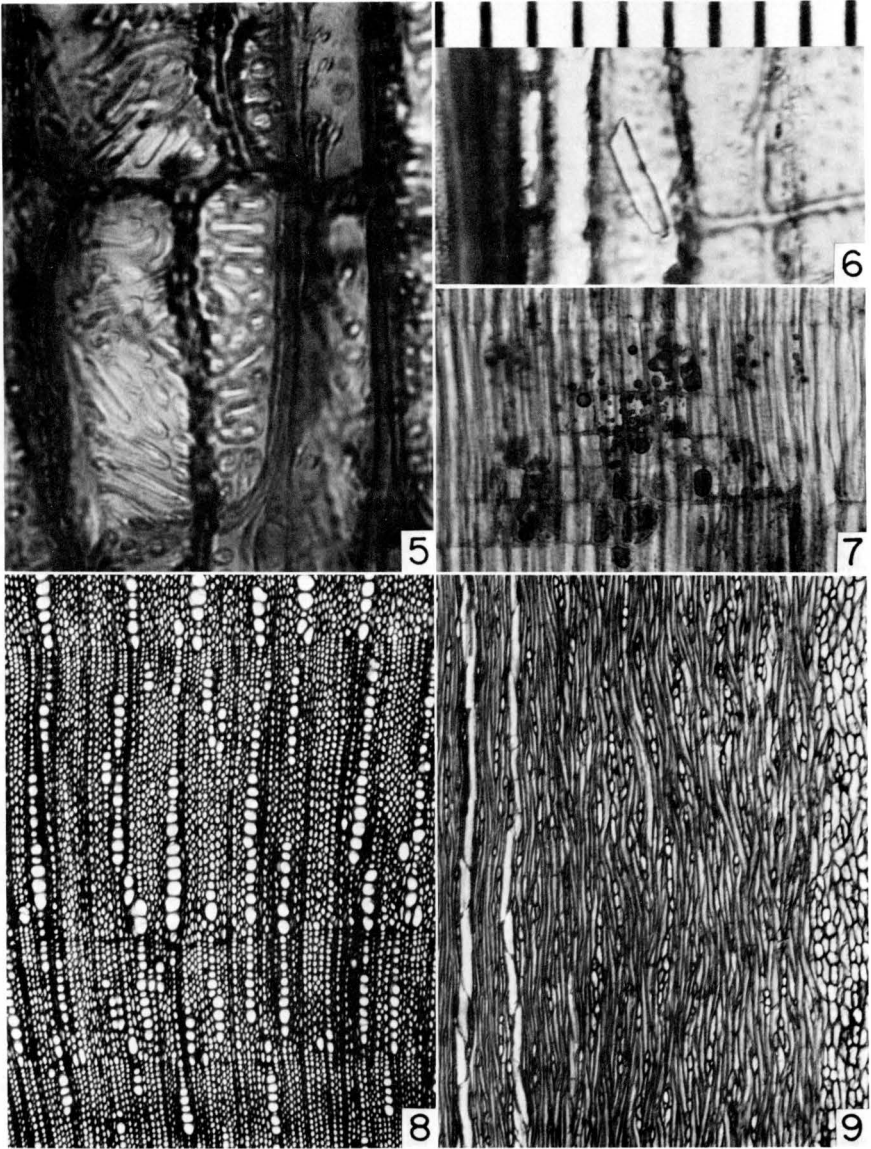
Growth rings.—The successive cambia do not seem to be annual productions. The occurrence of growth rings within each xylem band suggests this. Such growth rings can be seen in *Cyanostegia angustifolia* (Fig. 8). Less marked growth rings were also evident in *Lachnostachys eriobotrya* (Fig. 10), *Pityrodia lanuginosa* (Fig. 19), and *P. oldfieldii* (Fig. 23). The presence of two distinct phloem zones within a band of *C. lanceolata* (Fig. 4) is also suggestive of a growth-ring phenomenon. In the older phloem, the sieve tubes are entirely crushed but parenchyma cells with thick walls have enlarged to fill this zone; in the younger phloem, no such histological alteration is evident.

Vessels.—Degree of grouping of vessels, as shown in the figures above for each species, ranges widely within the woods sampled. A low degree of grouping is seen in *Lachnostachys eriobotrya* (Fig. 10), *Physopsis lachnostachys* (Fig. 14), and *Pityrodia oldfieldii* (Fig. 23). Larger groupings characterize *Cyanostegia lanceolata* (Fig. 1) and *Pityrodia lanceolata* (Fig. 29). A high degree of vessel aggregation occurs in *Cyanostegia angustifolia* (Fig. 8) and *Pityrodia bartlingii* (Fig. 17). In these two species, some long rows of vessels extend radially in chains of ten or more.

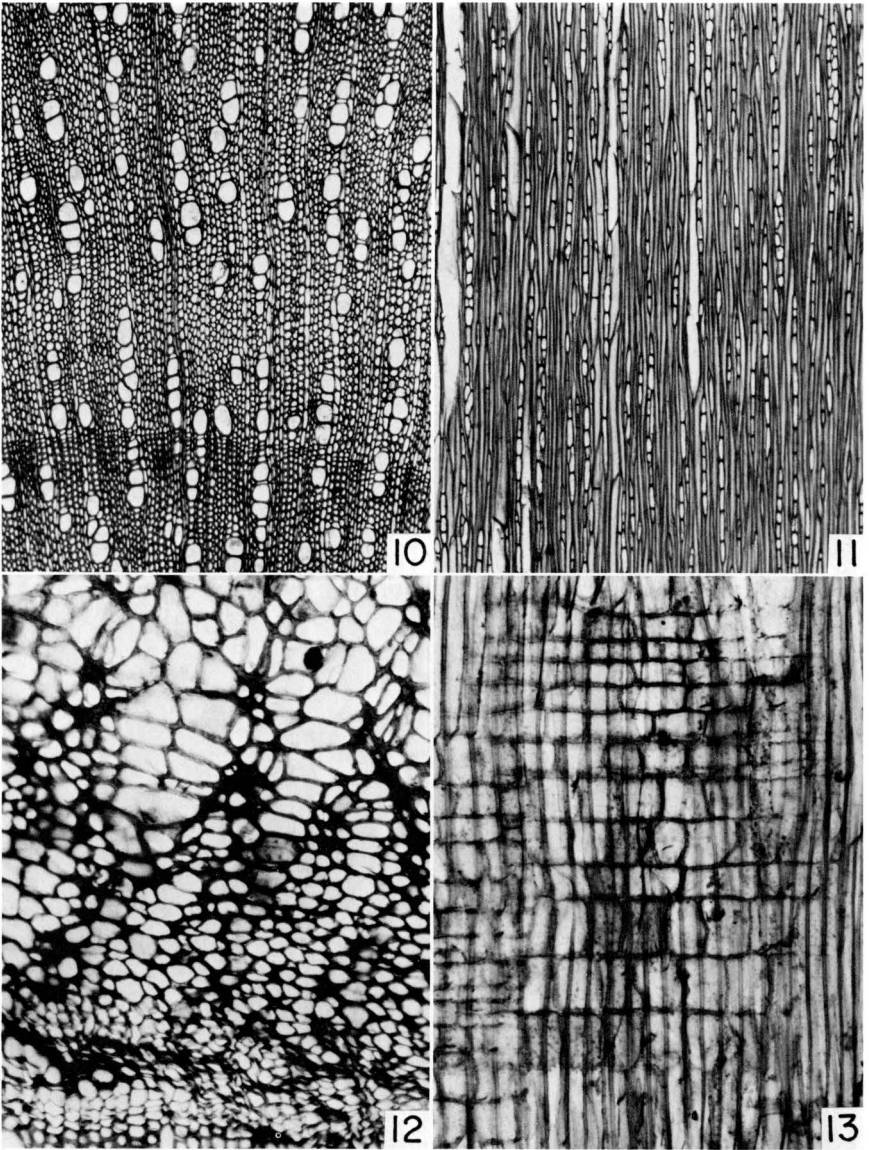
The figures for mean vessel diameter show a relatively narrow range, from 34 to 44 μm . Although the wood transections figured here show what appear to be wide variation from one species to another in diameter, this variation mostly occurs within rings, for a single vascular band can range from wider to narrower vessels. For example, Fig. 1 shows vessels much wider in the earlier portion of a band than in the later portion. Likewise, figures for vessel-element length and for density of vessels (vessels per sq.



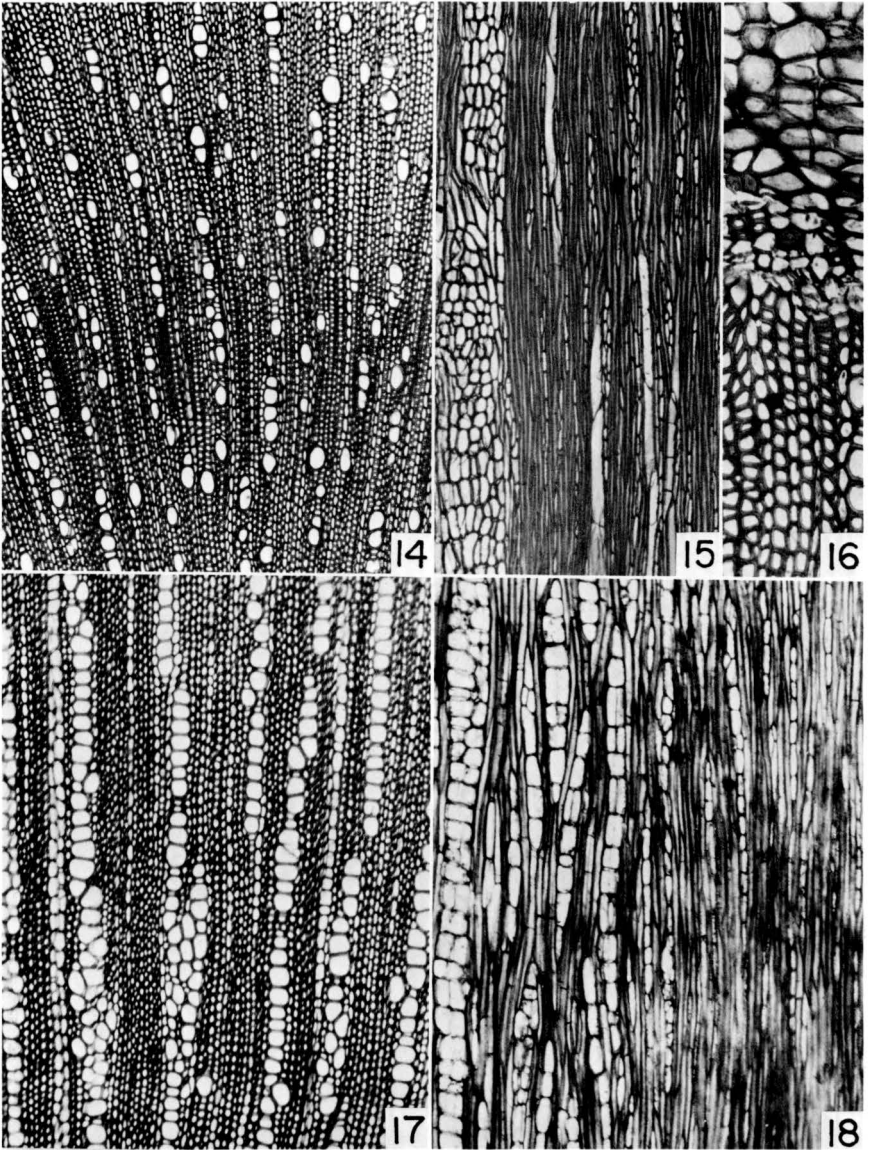
Figs. 1-4. Wood anatomy of *Cyanostegia lanceolata* (Carlquist 5905).—1. Transection, showing juncture of the products of two successive cambia; from top to bottom: xylem, parenchyma, phloem, xylem.—2. Tangential section; rays mostly uniseriate.—3. Radial section. Xylem at left, phloem (dark) center, parenchyma at right, showing that some files of ray cells are continuous, some not, across the phloem.—4. Transection. Subdivisions in parenchyma cells between the vascular bands can be seen, also survival of parenchyma cells in old secondary phloem. (1, 2, magnification scale above Fig. 2 [finest divisions = 10 μ m]; 3, 4, [divisions = 10 μ m]).



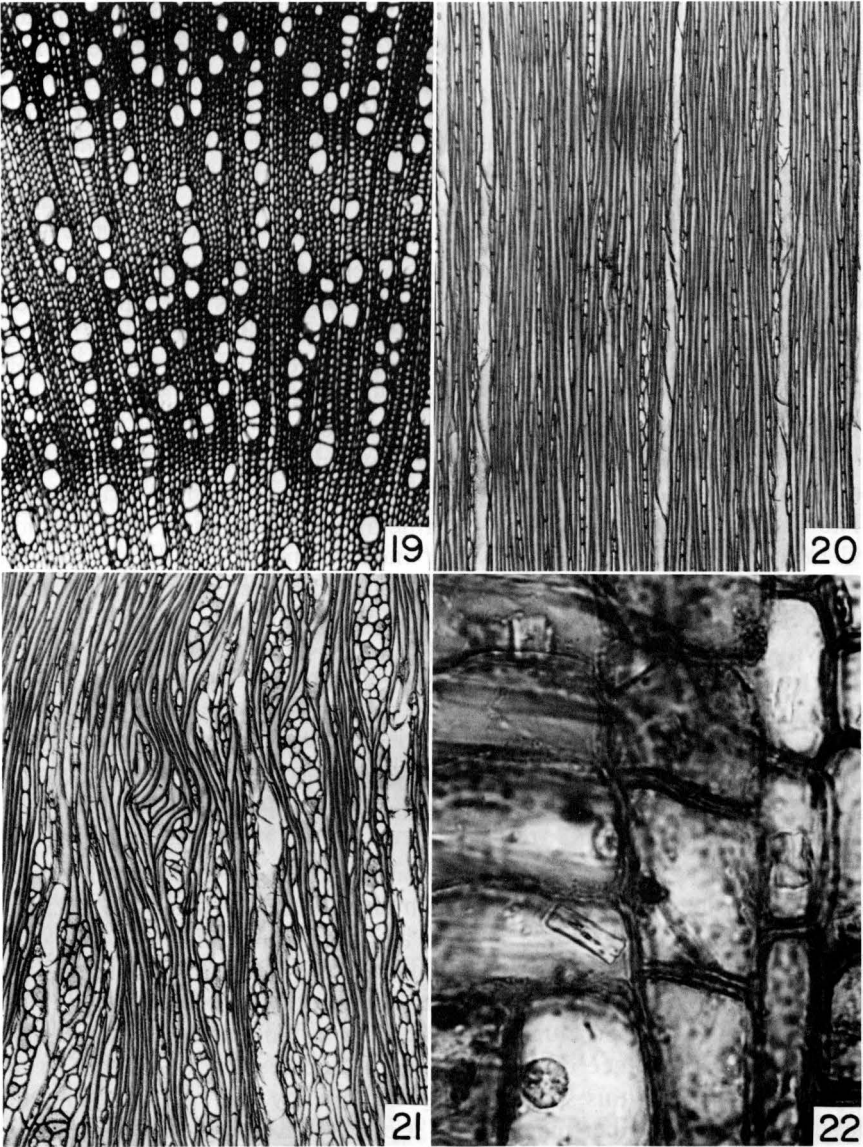
Figs. 5–9. Wood anatomy of *Cyanostegia lanceolata* (Carlquist 5905) (Figs. 5–7) and *C. angustifolia* (Carlquist s.n.) (Figs. 8–9).—5. Vessel-ray pitting from radial section.—6. Crystal from parenchyma cell.—7. Radial section, showing dark-staining deposits.—8. Transection. A growth ring is apparent.—9. Tangential section. Wide parenchyma zone at right is from parenchyma band where it abuts on xylem of the vascular arc. (5, 6, magnification scale above Fig. 6 [divisions = 10 μ m]; 7, scale above 3; 8, 9, scale above 2.)



Figs. 10–13. Wood anatomy of *Lachnostachys eriobotrya* (Carlquist 5896).—10. Transection. Very slight growth ring visible.—11. Tangential section. Both uniseriate and biseriate rays apparent.—12. Transection. Xylem at bottom, phloem above it. Upper half of photograph depicts the parenchyma between vascular bands.—13. Radial section. Procumbent ray cells above, erect ray cells below. Dark-staining compounds visible in some cells. (10, 11, scale above 2; 12, 13, scale above 3).



Figs. 14–18. Wood anatomy of *Physopsis lachnostachys* (Carlquist 5975) (Figs. 14–16) and *Pityrodia bartlingii* (Carlquist 5483) (Figs. 17–18).—14. Transection. Vessels not in large groups.—15. Tangential section. Parenchyma from between vascular bands is at left.—16. Juncture of parenchyma with vascular band (below). Phloem (center) contains fibers.—17. Transection. Long radial chains of vessels evident.—18. Tangential section. Larger-celled rays are in transition between ray of the vascular arc and parenchyma of the band between vascular arcs. (14, 15, 17, 18, magnification scale above 2; 16, scale above 3.)



Figs. 19–22. Wood anatomy of *Pityrodia lanuginosa* (Dunlop 4913) (Figs. 19–20) and *P. jamesii* (Carlquist 15417) (Figs. 21–22).—19. Transection. Variations in thickness of walls of fiber-tracheids evident.—20. Tangential section. Ray cells inconspicuous because of predominance of erect cells.—21. Tangential section. Wavy wood grain evident.—22. Radial section. Rhomboidal crystals and sphaerocrystals (lower left) present. (19, 20, magnification scale above 2; 22, scale above 6.)

mm.) show a rather moderate range within the family. However, as discussed below, even these rather moderate ranges seem amenable to ecological interpretations.

Lateral walls of vessels typically bear alternate pitting. However, some elongate pits were seen on vessel-ray interfaces (Fig. 5) in *Cyanostegia lanceolata* and *Pityrodia bartlingii*. Simple perforation plates and vessels circular in transectional outline characterize all the species in the present study.

Fiber-tracheids.—Imperforate tracheary elements must be called fiber-tracheids in Chloanthaceae. The diameters of pit borders are approximately half the length of the pit apertures. The only exception to this is in *Cyanostegia angustifolia*, in which some fully bordered pits were also observed on imperforate tracheary elements. Imperforate tracheary elements of Chloanthaceae are thus different from those of other Verbenaceae except for *Petrea volubilis* and *Tectona* spp., in which reduced pit borders have been found (Metcalf and Chalk 1950; Gottwald and Parameswaran 1980).

The walls of fiber-tracheids vary in thickness somewhat in chloanthoids, as data above show, but within rather narrow limits. The figures and the transections in this paper show that fiber-tracheids are not notably thick walled. The shrubby or subshrubby habit of Chloanthaceae may be correlated with moderate fiber-tracheid wall thickness.

The length of fiber-tracheids is roughly twice that of the vessel elements. This is a ratio typical of a specialized family of dicotyledons (Carlquist 1975).

Axial parenchyma.—Within the secondary xylem, axial parenchyma is vasicentric scanty. The parenchyma strands consist of two to three, occasionally four cells.

Ray parenchyma; parenchyma between vascular bands.—In some species, uniseriate rays outnumber the multiseriate rays (Fig. 2, 9, 11, 20). In others, multiseriate rays are at least as frequent as uniseriate rays (Fig. 15, 21, 31). Rays are often inconspicuous because of the narrowness of ray cells and their tendency toward erectness rather than procumbency. The only species in which procumbent ray cells are abundant is *P. lanceolata* (Fig. 31). The abundance of ray cells in this species can be related to the arborescent nature of this species, for procumbency of a ray cells generally characterizes the woodier members of a phylad of dicotyledons, erectness the herbaceous species, with increasing procumbency during the ontogeny of any stem (Carlquist 1962). In the species other than *Pityrodia lanceolata*, procumbent cells are less frequent than erect cells (Fig. 13) or rare (Fig. 3).

The pattern of ray cell lineages can continue from secondary xylem through secondary phloem and into the bands of parenchyma which intervene between the arcs of vascular tissue (Fig. 3). More often, cell lineages do not continue across this sequence, however. The fact that sequences

may be found suggests that there is an interrelationship between the ontogeny of the cambium and the succeeding band, albeit not a continuous and direct one as with a normal cambium. Transections also hint at this continuity (Fig. 4).

Where ray parenchyma of the first-formed secondary xylem of each band abuts on a band of parenchyma (Fig. 4), there is a continuity in cell type if not in cell lineage as well. One feature of the band parenchyma is sometimes carried into the ray parenchyma: the tendency for radially oriented subdivisions to occur. Thus, in Fig. 15 and 18, divisions can be seen in the rays with larger cells—rays which are close to the transition into the bands of parenchyma intervening between vascular arcs. When one views transections of band parenchyma, one also sees subdivisions (Fig. 4, 12). These subdivisions seem in part best interpreted as related to increase in circumference by the stem.

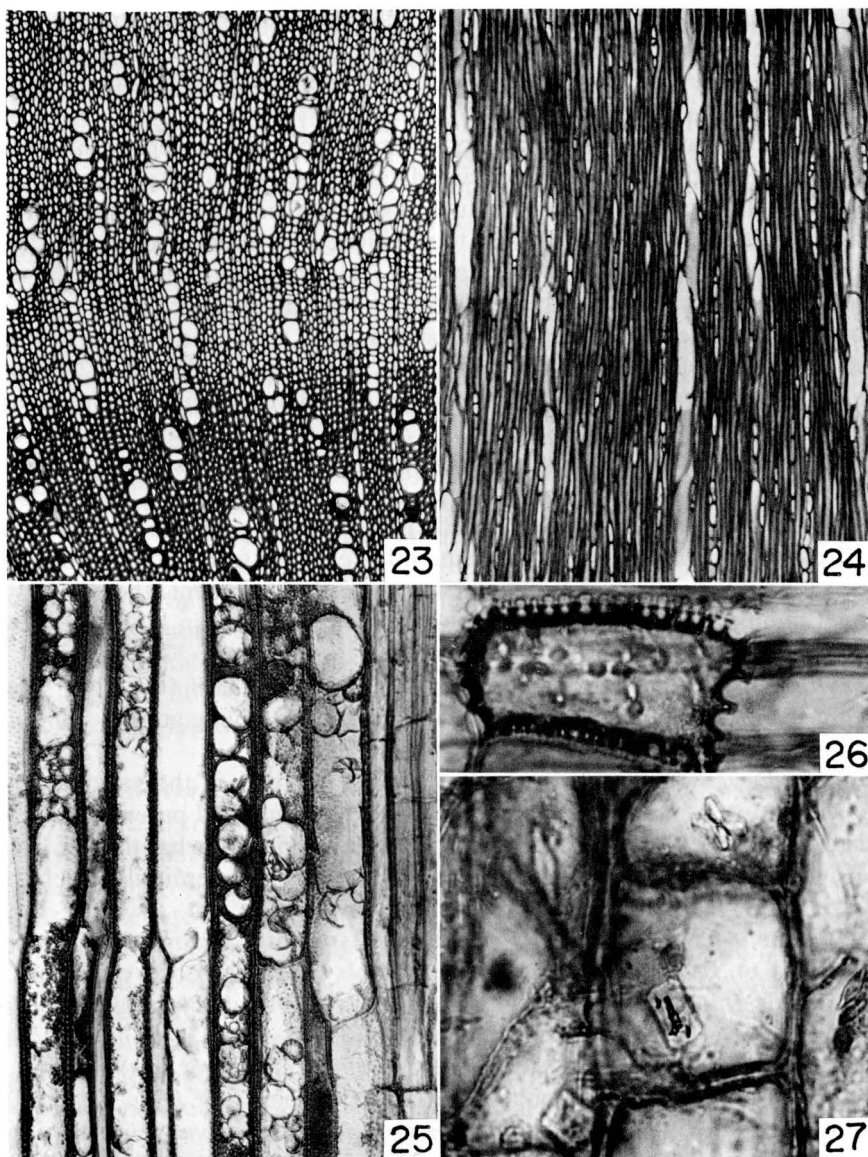
Ray cell walls are not notably thick. Simple pits are present on many ray cells. However, some ray cells can bear bordered pits (Fig. 26). Bordered pits were observed on some ray cells of all species studied. Bordered ray cell pits will probably be more frequently reported from woods when pits in sectional view on radial sections are studied. At present, there is only a small number of observations on bordered ray cell pits in literature on dicotyledon woods.

Tyloses.—Tyloses are abundant in *Pityrodia oldfieldii* (Fig. 25). These occur in older vessels, either with or without dark-staining gummy contents. Tyloses were not seen in the other species.

Secondary phloem.—As secondary phloem matures in the vascular arcs, sieve tube elements and companion cells are crushed and parenchyma cells enlarge (Fig. 4, 12). The parenchyma cells develop somewhat thicker walls. In only one species, *Physopsis lachnostachys*, were sclereidlike fibers observed to develop in phloem.

Crystals.—Crystals were observed to be sparse in *Cyanostegia lanceolata* (Fig. 6). Only in *Pityrodia* were crystals otherwise observed. Narrow rhomboids with pointed or blunt ends were observed in *P. lanceolata* (Fig. 30). A great variety of rhomboidal crystals were observed in *P. jamesii* (Fig. 22, 27); narrow rhomboids were present (Fig. 27, upper left) as well as rhomboids square or rectangular as seen in side view (e.g., Fig. 22; Fig. 27, below). Aggregations of crystals into a group were observed (Fig. 27, upper right) and sphaerocrystals were observed (Fig. 22, lower left). The same range was noted for *P. lanuginosa*, in which crystals occurred more sparsely. Crystals were observed only in the ray cells of the chloanthoids. Although rhomboidal crystals have been observed in *Petraea* and *Tectona*, the remainder of Verbenaceae (s.s.) have needlelike crystals (Metcalf and Chalk 1950).

Gummy deposits.—At least a few droplets of dark-staining compounds



Figs. 23–27. Wood anatomy of *Pityrodia oldfieldii* (Carlquist 5899) (Figs. 23–26) and *P. jamesii* (Carlquist 15417) (Fig. 27).—23. Transection. Minor growth ring variations evident.—24. Tangential section. Most rays are uniseriate.—25. Radial section. Tyloses and dark-staining compounds evident.—26. Ray cells from radial section. Dark-staining compound shows outlines of pits; bordered pits above.—27. Crystals from ray cells of radial section. A tetrad of crystals can be seen above. (23, 24, magnification scale above 2; 25, scale above 3; 27, scale above 6.)



Figs. 28–31. *Pityrodia lanceolata* (Carlquist 15450).—28. Branch showing leaves and flowers.—29. Transection, showing juncture between two successive vascular bands. Phloem strands are mostly shriveled.—30. Ray cells from radial sections; rhomboidal crystals at upper right and lower left.—31. Tangential section. Multiseriate rays are conspicuous. (28, $\times 1.2$; 29, 31, magnifications scale above 2; 30, scale above 6.)

could be detected in ray cells of Chloanthaceae (Fig. 30). In some species, such as *Cyanostegia angustifolia* (Fig. 7) and *Pityrodia oldfieldii* (Fig. 26), the deposits are more massive. Deposits in vessels were abundant only in *P. oldfieldii* (Fig. 25).

Ecological Interpretations

As noted in the Introduction, wood anatomy of Chloanthaceae does not exhibit a wide range of diversity quantitatively. This is suggestive of adaptation of the group to a relatively narrow range of relatively dry habitats. The figures relating to vessel elements are also expressed in terms of ratios or indices which I have called Vulnerability (vessel diameter divided by vessels per sq. mm.) and Mesomorphy (vulnerability multiplied by vessel-element length), as mentioned earlier (Carlquist 1977). One must take into account the possibility that the relatively limited range for figures in these indices (see Quantitative Data) is accounted for by intervention of leaves in mediating transpirational loss, so that the formulation of a wood is not as closely keyed to the ecology of a site as it would be in a group with broad, thin leaves sparsely clad with trichomes and with low diffusive resistance ratings. Leaf surface areas do roughly correlate with the mesomorphy index, however, with highest values in the largest-leaved species, *P. lanceolata*, and lowest values in the smallest-leaved species, *Cyanostegia angustifolia*, which was collected in the Victoria Desert. All of the vulnerability values for the family are low, compared to other dicotyledon groups, suggesting that basically this is a group adapted to dry habitats. The species with the highest mesomorphy values are the three *Pityrodias* from the Arnhem Land sandstones, where humidity is high and annual rainfall exceeds 50 inches per year (Atlas of Australian Resources, 1953). However, even this area has a dry winter season. Areas in southwestern Australia are more severe, because rainfall is somewhat less, humidity is generally lower, and the dry season coincides with the hot summer months. One cannot attribute statistical significance to these figures: probably in no way can the complex interaction of plant parts which act conjunctively be analyzed quantitatively so as to provide consistent statistical significance. Oever, Baas and Zandee (1981) seem to require a mathematic precision and predictability of the V and M indices which is unreasonable: the indices merely show in vague ways where along the continuum from xeric to mesic a wood lies. One must remember that there is more than one kind of a mesic habitat also. However, in chloanthoids as in other groups, these indices show trends of a clear direction and illustrate that wood structure frequently bears a close relationship to habitat. The trends for the groups for which these indices have been constructed are anything but random. The fact that in group after group the trends are similar with respect to a span between xeromorphy

and mesomorphy can itself be considered a form of significance, for it is like an experimental material subdivided into replications. The statistical odds of numerous groups independently showing no parallel patterns for correlation between quantitative wood features and ecology of species is virtually nil: meaningful patterns do emerge. None of the groups shows anything like a random distribution of the values with respect to their component species and the ecology of those species.

The fact that tracheids, rather than fiber-tracheids occur in *Cyanostegia angustifolia* may be related to an ecological factor, dryness. As noted elsewhere in the case of Mojave Desert shrubs (Carlquist 1980), tracheids confer safety because air embolisms are localized if they form during extreme water stress, so persistence of woods with tracheids in dry regions, such as the Victoria Desert area where I collected *C. angustifolia*, is not surprising.

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Footnote

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